

The identity, affinities, and staminate floral structure of *Pandanus pendulinus* Martelli (Pandanaceae)

BENJAMIN C. STONE

Department of Botany, University of Malaya, Kuala Lumpur, Malaysia

and

KIM-LANG HUYNH

Botanical Institute, University of Neuchâtel, Switzerland

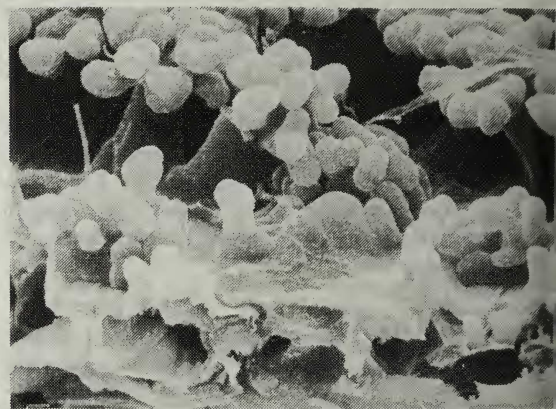
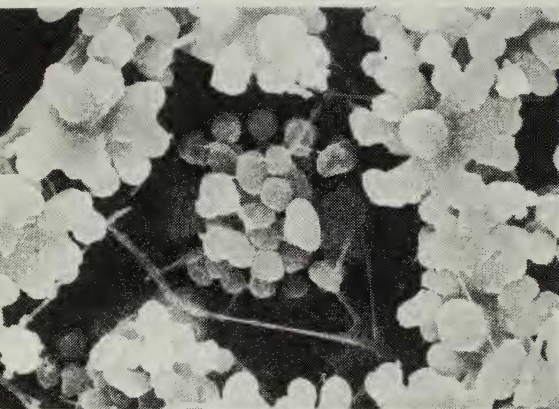
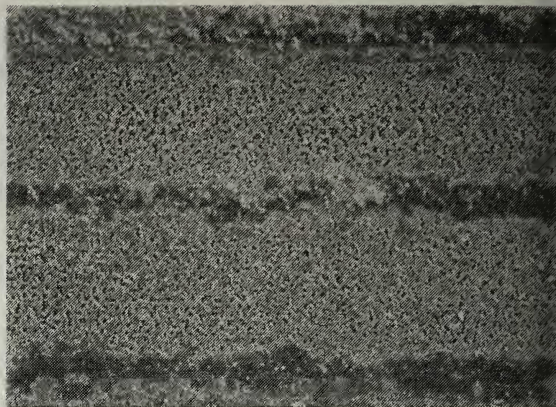
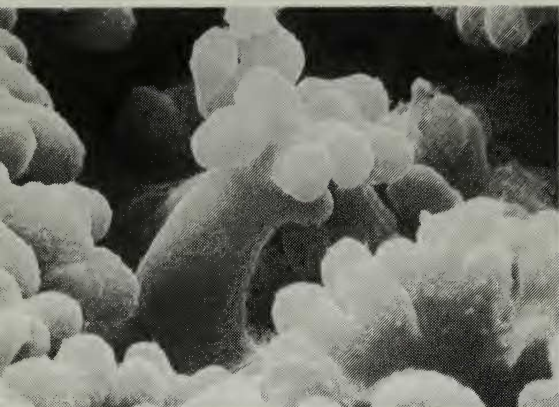
Abstract

The leaves and male flower of *Pandanus pendulinus*, an obscure species known so far only from one collection (the type), have been studied from both gross and micromorphological viewpoints using both light and scanning electron microscopy. The species, which was originally placed in section *Acrostigma*, is reassigned on the basis of the characters observed, to subgenus *Lophostigma*, but it still remains uncertain in its closer relationships and cannot yet be assigned to a particular section within this subgenus.

Introduction

In 1925-26 the Arnold Arboretum sponsored a botanical expedition to New Guinea. The collector was Leonard J. Brass, who continued in later years and became perhaps the most capable, persistent and knowledgeable field botanist ever to have worked in New Guinea. On this early trip, Brass collected chiefly in the Gulf district of Papua, in the region of the Vailala River about 150 miles north-west of Port Moresby, and also in the Laloki River area along the coast between Port Moresby and Redscan Bay. C.T. White, the government botanist in Brisbane, undertook the identification of the materials collected, assisted by various specialists, and the Pandanaceae were consigned for study to the then authority, U. Martelli. In his report, Martelli (1929) described six new species of *Pandanus* from the collections made by Brass. All but one of these have subsequently been collected again, if only once or twice. One of them, however, *Pandanus pendulinus*, has never again been collected.

During 1971 when the senior author (B.C.S.) was studying the New Guinea pandans in the field through the courtesy of the Lae Herbarium, the opportunity was taken to work around Ihu, on the Vailala River, in the hope of obtaining this and other species in the area originally explored by Brass. During this visit many collections were made and one new species (*Pandanus columbiformis*) was discovered (Stone 1974a). Three of Martelli's species were recollected (*Pandanus leptocarpus*, *P. scabribracteatus*, both from Ihu, and *P. brassii*, from another locality), but *P. pendulinus* was not found and is still known only from the original type collection.



Plates 1-4, *Pandanus pendulinus*: 1 (top left) — leaf, papilla of polar cell from abaxial face, with lobulate apex at centre, x 2263; 2 (top right) — leaf, abaxial face (the darker, narrower bands are the non-stomatiferous zones, x 31); 3 (bottom left) — leaf, abaxial face (in centre stomate with branched apices of papillae of polar cell, flanked by a lateral cell revealed by its five simple papillae; in periphery, dentritic papillae from neighbouring cells forming a "roof", x 1293); 4 (bottom right) — leaf, transverse section, abaxial side (in right-hand third, epidermis and hypodermis, with two transversely cut stomata respectively at top and bottom, each with guard cells, lateral cells with simple papillae, and at left the branched apex of papilla from polar cell; in left side two-thirds, abaxial face with lobulate papillae of non-stomatic epidermal cells, x 1422).

Thus *Pandanus pendulinus* has remained an enigma, particularly because the sole collection was a staminate flowering specimen, with the spikes and flowers in a meagre and rather poor state of preservation, and with inadequate materials of the vegetative parts. Martelli (1929) assigned this species to section *Acrostigma*. However, his description of the stamens as separately standing on bulbils of the spike axis and with "filamento longissimo, tenuissimo, 2.5 mm longo" reveals that there could be no affinity with this or any other section of subgenus *Acrostigma*.

An examination of the type specimen, preserved in the herbaria of the Arnold Arboretum of Harvard University and the Botanical Institute of the University of Firenze, showed that the spikes were heavily damaged and most stamens broken, only a few anthers being found still bearing the apiculus. Luckily a few intact stamens still attached to the spike axis were found, these permitting a more complete understanding of their structure. Tangential microtome sections of portions of the spike made it possible also to ascertain the arrangement of the stamens, and thus the identification of the floral unit on the spike axis. Anatomy of the stamens as well as of the leaf was investigated. For a better comprehension of the taxonomic value of leaf micromorphology, see Huynh (1974).

Description of the species

Pandanus pendulinus Martelli, J. Arn. Arb. 10: 142, pl. 18B, 1929. Kanehira, Bot. Mag. Tokyo 54: 258. 1940.

A tree 7-8 m tall, the trunk spiny, 20 cm in diameter, at base with proproots to 3 m long, 5 cm thick, stilt-like, fibrous, densely spiny with antrorse spines. Leaves broadly linear, 300-350 cm long or more, to 11.5 cm wide, gradually attenuate and slightly acuminate toward the apex, there almost flat but toward the base deeply channelled, thickly and rigidly coriaceous, the undersurface glaucescent, the longitudinal veins scarcely to somewhat prominent, smoother than the inter-vein bands (zonate). Leaf margins prickly; toward the base ... (no data); above the base but below the middle, with prickles 1.5-2 mm long, 4-9 mm apart, all antrorse, the prickles broad, its distal edge straight and perpendicular to the leaf-margin, at apex abruptly deflected forward as a dark, sharp tip; near the leaf middle, the marginal prickles 1-1.4 mm long, 5-11 mm apart, antrorse; near the apex, the prickles more appressed, more deltoid, 0.5-1 mm long, 1-3 mm apart. Midrib dorsally carinate, acute, near the base ... (no data); above base but below middle, with very small antrorse depressed prickles 0.25-0.4 mm long, 2-8 mm apart; near but below the apex, the prickles yet smaller and more appressed; along apex, the prickles absent or reduced to minute nubs less than 0.1 mm high, blunt. Apical ventral pleats of leaf rounded, unarmed in our scanty material. Longitudinal nerves about 150 per leaf, 0.4 mm apart nearest margins, to 1.1 mm apart near the midrib, light brown. *In microscope*: abaxial epidermis divided into broad stomatiferous zones and very narrow non-stomatiferous zones, stomates about 18 μ long, of class VII (polar cells each with an apically dendritic papilla), papillae of polar cells c. 16 μ long; lateral cells with 5 or 6 simple papillae in line, nonstomatic cells each with a dendritic (Class VII) or branched or lobed (Class VI) papilla, the latter about 15 μ in diameter; chlorenchyma (on both sides) almost uninterrupted at the longitudinal

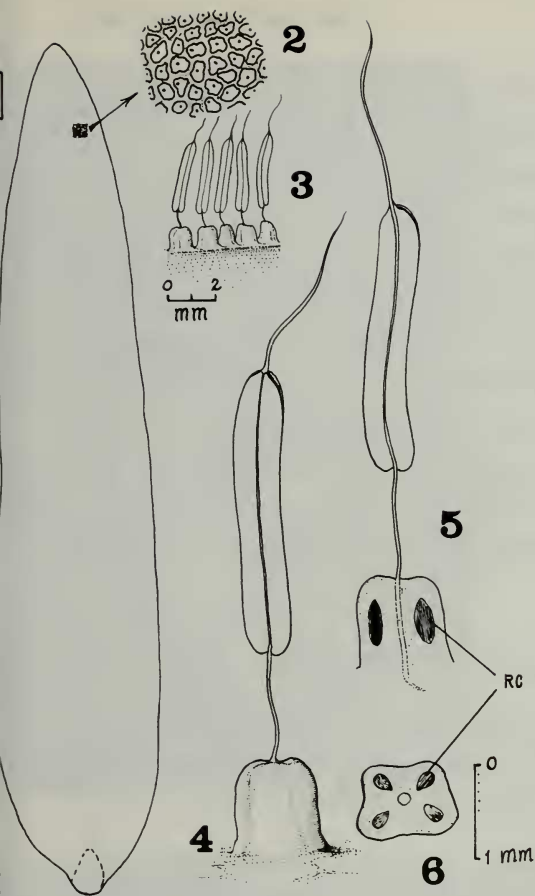
nerves, hypodermis with 3 or 4 cell-layers, spongy tissue with 0 or 1 cell-layer; first cell-layer of hypodermis with crystal cells in both sides, but these most dense at the longitudinal nerves in the abaxial side. (Plates 1, 2, 3 & 4).

Staminate inflorescence pendulous, over 1 m long, with many narrow spathes; main rachis to 3 cm diameter; upper internodes 7 cm long or less; lower spathes over 50 cm long, over 3 cm wide; lanceolate; upper spathes linear-lanceolate, gradually acuminate, navicular, narrow, coriaceous, margins apparently (distally) minutely prickly; apical ventral pleats with a few prickles; coloration red. Spikes 5-7, up to 20 cm long, 4 cm broad at base, narrowed to apex, somewhat flattened, covered with the very numerous crowded stamens, subsessile. Stamens arranged in floral units of elliptical form consisting of 7 to 9 stamens without a column, each stamen with a bulbiform filament (brown in our material) about 1 mm long and 1 mm broad, rounded at the apex, variously subangular in section, connate at base, with a single vascular bundle and 3-5 raphid cells around it; anthers c. 3 mm long, 0.5 mm wide, oblong, rounded at base and apex, 2-celled when mature, linked to the filament by an extremely slender basal prolongation of the connective about 2.5 mm long, about 0.05 mm thick, smooth translucent, devoid of both raphid cells and crystal cells and without endothecial sclerification; walls of loculi devoid of both raphid cells and crystal cells, completely opened at full dehiscence, with an endothecium generally 2-layered at the middle and an extremely thin epidermis with elongate cells; connective endothecially sclerified throughout except for a thin portion around the vascular bundle, devoid of raphid cells and crystal cells or rarely with 1 or 2 raphid cells; apiculus flagelliform, to 2.5 mm long, 0.05 mm thick, smooth translucent, vascularized in the lower half, endothecially sclerified very slightly at base, with 1 or rarely 2 raphid cells; pollen smooth, about 17 x 12 x 10 μ , pore apical, tectum complete. (Figs 1-6).

PAPUA NEW GUINEA: Ihu, on the Vailala River, 24 February 1926, *L. J. Brass* 1053 (A! holotype, FI! isotype).

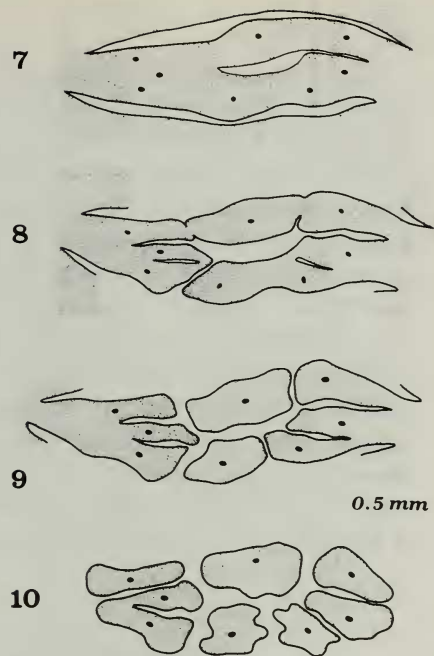
Observations on the structure of the staminate flower

When observed from above, the stamens of *P. pendulinus* appear to be free on the spike axis. However, serial tangential sections reveal that they are arranged in distinct floral units, which we presume to be the staminate flowers. In the lowermost sections, vascular bundles are horizontal and belong to the spike axis. From sections close to the surface of the spike axis, all vascular bundles appear distinct and vertical and belong to the staminate flowers. In the next section above, several gaps more or less parallel with the spike axis appear, each marking a lateral boundary of the flower. In the next higher section these gaps are wider; and shorter gaps, more or less parallel with them, occur between them. Thus there is a more or less elliptic uninterrupted structure with 7 to 9 vascular bundles (Fig. 7, where 8 such bundles are visible); this is formed by the connate bases of the filaments of a single floral unit. In the next section above, the filaments appear between radial gaps in the elliptical area (Figs. 8-10). The filaments are variously connate basally, but become separate at a point about 80-300 μ from the surface of the spike axis.



Figs. 1-12: *Pandanus pendulinus*.

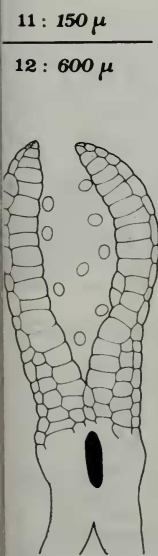
Figs. 1-6: Details of staminate spike and stamens; — 1: staminate spike; — 2: detail of portion of the surface of the spike, with only the filaments shown; — 3, 4: stamens; — 5: stamen with filament in l.s. (RC = raphid cells); — 6: filament in t.s.



Figs. 7-10: T.s. of staminate flower at distances of 45 μ , 90 μ , 120 μ and 255 μ from surface of the spike axis (dark points = each a vascular bundle; sections, 15 μ thick).

Fig. 11: T.s. of an anther (sections, 15 μ thick; dotted areas = endothecially sclerified parts; large ellipse = vascular bundle; smaller ellipses = pollen grains).

Fig. 12: Apex of anther showing apiculus (dotted area = endothecially sclerified part; middle dark line = vascular bundle; note raphid cell at apex of apiculus).



11

12

Transverse sections of the anthers show them to be elongated and to consist of four walls in two pairs, each pair lying close together and enclosing several pollen grains (Fig. 11, in which only one pair of walls is shown). This structure could be mistaken for a loculus, but in reality, because the loculi open completely in later dehiscence, the locular walls recurve so far that each almost touches the corresponding wall of the other loculus, thus forming a "false" chamber in which pollen grains may be trapped. In the same figure, the pollen grains are shown trapped in the "false" chamber. This can be established by locating the thickest cell-layer of the endothecium in each wall, which is always at the inner side. The outermost cell-layer of the endothecium (i.e. the layer immediately beneath the epidermis) is always the thickest in *Pandanus* (e.g. Plate 5), as has been ascertained in numerous species which have been studied (Huynh, 1982) and in which the epidermis can be identified by the presence of a thick visible cuticle. In the case of *P. pendulinus*, the anther wall cuticle is imperceptible in light microscopy; in fact, even the epidermis is invisible, as it is very thin and closely applied to the endothecium (Plate 6).

On the taxonomic position of *Pandanus pendulinus*

In a comparative survey of the very variable staminate flowers of *Pandanus*, we have studied most species of which staminate collections have been obtained, these pertaining to 49 different generic sections (Stone, 1974b; Huynh, 1982).

Generally speaking, each natural section has a characteristic staminate flower, and in those sections which are closely related, a similar floral structure has been observed. This general survey provides grounds for a confident decision on the taxonomic position and affinities of *Pandanus pendulinus*, and also permits us to homologize the different parts of the staminate flower of this species with those of other species.

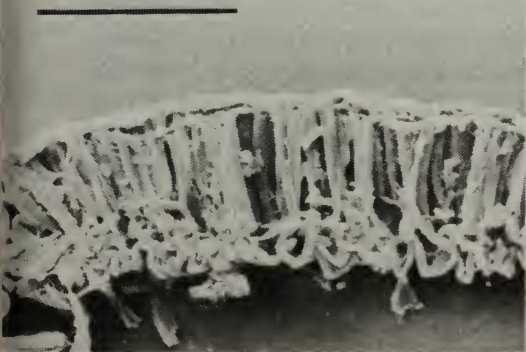
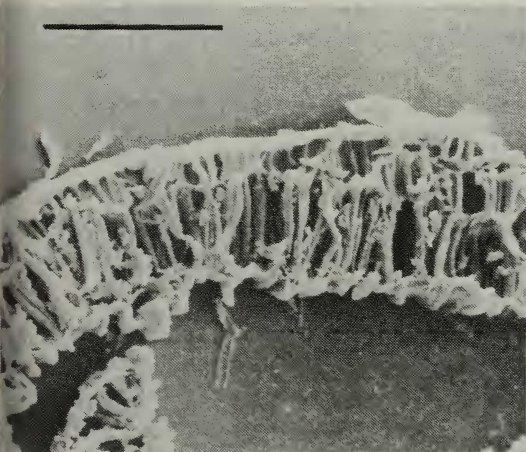
An outstanding feature of the staminate flower of *Pandanus pendulinus* is the arrangement of the 7 to 9 filaments in units of elliptical outline which are attached to the spike axis directly, that is without the usual intervening column (stemonophore). Moreover the filaments are bulbiform and connate at the base, and each is linked to the anther by a filiform, flexible, translucent basal prolongation of the connective. Staminate flowers of this configuration have until now only been observed in section *Maysops* of subgenus *Lophostigma*.

Another important feature of the staminate flower of *P. pendulinus* is the very long anther apiculus, which may reach a length of 2.5 mm. Apiculi of this length are rather unusual in the genus, although they are known in section *Karuka* (subgenus *Lophostigma*) and in one or two species of section *Rykia* (subgenus *Rykia*). Other characteristics clearly eliminate the possibility of a close relationship of *P. pendulinus* with any species or section outside subgenus *Lophostigma*, however. The staminate flower structure of *P. pendulinus* strongly indicates that its taxonomic position should be in subgenus *Lophostigma*, near to but not within section *Maysops*.



Plate 5 (top left) — *Pandanus zea* St John, type-species of section *Maysops* (Cape York, 7. VI. 1948, Brass 19069); transverse section of an anther wall at midlevel (note the epidermis at left, in part with somewhat inflated cells, and the endothecium with two cell-layers and lignin thickenings, and compare with Pl. 6; scale: 50 μ).

Plates 6-8, *Pandanus pendulinus*: 6 (top centre) — anther wall, transverse section, from the type specimen, scale: 50 μ ; 7 (top right) — apices of filaments and basal prolongations of connectives, x 42; 8 (bottom left) — pollen grains, x 1896.



Other facts corroborate this conclusion. The pollen of *P. pendulinus* is provided with a smooth and complete tectum (terminology according to the International Conference on Palynology, Paris, 1975) (Plate 8). Pollen of this type has been observed in the following subgenera: *Acrostigma*, *Kurzia*, and *Lophostigma*. It occurs most frequently, however, in the sections *Lophostigma*, *Barrotia*, *Maysops*, *Karuka*, and *Asterostigma*, all of subgenus *Lophostigma*.

Characters of other organs also support the assignment of *P. pendulinus* to subgenus *Lophostigma*. For example, the leaves have an obscurely zonate abaxial face, stomates of class VII, and almost uninterrupted chlorenchyma in both adaxial and abaxial faces. Such leaves have been observed also in subgenus *Lophostigma*, e.g. in species of section *Maysops* (Huynh, 1976). Finally there is the biogeographic association: New Guinea is richest in sections of subgenus *Lophostigma* (Stone, 1974b).

Despite the evident affinity of *P. pendulinus* with sections *Maysops* and *Karuka*, it cannot be assigned to either of these. Nor is there any more likely section for it among those belonging to subgenus *Lophostigma*. Of the distinctive characters of *P. pendulinus*, the long filiform translucent anther apiculus is particularly noteworthy. It suggests some isolation of the species. The filiform translucent part between the anther and the bulbiform process of the stamen provides another peculiarity of the species. That part should be regarded as the basal prolongation of the connective, since it is also filiform and translucent. Therefore the bulbiform process is the filament, and this is also indicated by its colour (brown, in dry material) and its solitary vascular bundle, characters of filaments of *Pandanus* in general. In *P. pendulinus* this basal prolongation of the connective may be up to 2.5 mm long, which is a most unusual feature. The connective is quite, or almost, devoid of raphid cells, another unusual feature, like the apiculus, which has only a slight amount of endothelial sclerification at the base.

In contrast, in section *Maysops* the basal prolongation of the connective only extends to 0.4 mm (so far as yet known); the connective is rich in raphid cells; the apiculus likewise is rich in raphid cells and moreover is endothecially sclerified from base to apex (Huynh, 1982).

Of the other sections of subgenus *Lophostigma*, those which are endemic to New Caledonia can probably be eliminated as potential allocations for *P. pendulinus*, since it is known only from Papua New Guinea, and also because in those New Caledonian species of the subgenus in which the staminate flowers are known, the floral structure is quite different (the stemonophore terminates in a peltate apex, the stamens have no filaments and are subracemously attached to the stemonophore: Stone, 1974b; Huynh, 1982). Therefore on biogeographic grounds only the sections *Perrya*, *Metamaysops*, *Megastigma*, *Karuka* and *Liniobtutus* appear to be possible taxonomic sites for *P. pendulinus*. (Section *Paralophostigma*, originally included in subgenus *Lophostigma*, is now assigned to subgenus *Kurzia*). Of the sections mentioned, *Karuka* and *Liniobtutus* can be ruled out. In section *Karuka*, the staminate flower is normally provided with a central staminode (or pistillode; its nature is not quite certain); the filaments are fused from base to apex and lack raphid cells; the connective and apiculus are rich in raphid cells; and the dorsal face

of the distal part of the apiculus is papillate, whereas the ventral face has some epidermal cells with thick lignified walls (Huynh, 1982). Moreover, the leaves have abaxial stomates of Class V (Huynh, 1976). In section *Liniobtutus*, the staminate flower has a stemonophore, the stamens have no basal prolongation of the connective, the anther loculi are not completely opened out by dehiscence, and the pollen is spinulose (Huynh, 1982). Moreover, the leaves have abaxial stomates of Class II or III (Huynh, 1976). As to sections *Perrya*, *Metamaysops*, and *Megastigma*, the staminate plants remain unknown.

Thus it appears that *Pandanus pendulinus* represents a previously unrecognized and still undescribed section of subgenus *Lophostigma*.

Acknowledgements

We expressly thank the directors of the herbaria of the Arnold Arboretum, Harvard University (A) and the Botanical Institute, University of Firenze (FI) for access to the specimens studied, and both the Museum of Comparative Zoology, Harvard University, and the Zoological Institute, University of Neuchâtel, for the use of the scanning electron microscope facilities. The SEM operator in the former institute, Ed Seling, is particularly thanked for his skilful assistance (resulting in our Plates 1-4, 7&8). The Arnold Arboretum is thanked for its support of this project which was carried out while the senior author was on sabbatical leave and based at the Arboretum as a Mercer Fellow.

References

- Huynh, K.-L. 1974. La morphologie microscopique de la feuille et la taxonomie du genre *Pandanus*. I. Aperçu général sur les caractères micromorphologiques de la feuille du genre *Pandanus* et leur valeur taxonomique. *Bot. Jahrb. Syst.* 94: 190-256.
- 1976. La morphologie microscopique de la feuille et la taxonomie du genre *Pandanus*. III. Le sous-genre *Lophostigma*. *Bot. Jahrb. Syst.* 97: 72-119.
- 1982. La fleur mâle de quelques espèces de *Pandanus* subg. *Lophostigma* (Pandanaceae) et sa signification taxonomique, phylogénique, et évolutive. *Beitr. Biol. Pflanzen* 57 (in press).
- Martelli, U. 1929. The Pandanaceae collected for the Arnold Arboretum by L. J. Brass in New Guinea, *J. Arn. Arb.* 10: 137-42.
- Stone, B.C. 1974a. Studies in Malesian Pandanaceae XIII. New and noteworthy Pandanaceae from Papuasias. *Contrib. Herb. Austral.* 4: 7-40.
- 1974b. Towards an improved infrageneric classification in *Pandanus* (Pandanaceae). *Bot. Jahrb. Syst.* 94: 459-540.